REGULATION OF CASTE IN SOCIAL HYMENOPTERA*

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Communal life in the social Hymenoptera (wasps, bees, and ants) is so completely integrated that the nature and the operation of the mechanisms which in each generation cause the offspring of a mated female to develop into several castes with each caste relatively constant in numbers are highly cryptic.

In the Hymenoptera, however, the framework of social organization apparently consists of the interaction of two phenomena, the environmental control of sex and the environmental control of caste (Flanders, 1946). This interaction is the basis of the following analysis of the hymenopterous society.

The primary effect of the interrelation of sex and caste control is the limitation of true castes to the female sex. Because of this limitation it is logical to assume that the circumstances that initiate the fertilization of the egg also initate caste formation. This assumption seems to be verified by the existence of the necessary mechanisms (Flanders, 1953). The following discussion therefore describes the critical mechanisms involved and advances certain hypotheses concerning the methods by which these mechanisms operate to regulate caste ratios.

The essential physiological mechanisms involved in the regulation of caste ratios include those involved in the control of sex—the spermatheca, the spermathecal gland, and the spermathecal duct—the spermatheca having a sperm storage capacity sufficient for the fertilization of all eggs deposited, the spermathecal gland having a capacity for producing sperm-activating secretion sufficient to permit the fertilization of all eggs regardless of the rate of oviposition, and the sperm duct having a lumen adapted to holding several sperms enroute to the oviduct (Flanders, 1939).

These mechanisms become essential factors in sex and caste control when, as in the social Hymenoptera, sex determination is haplodiploid (unfertilized eggs usually becoming males and fer-

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tilized eggs becoming females), ovulation is environmentally induced, the spermathecal gland is responsive only to environmental stimuli, and oviposition by the queen is largely limited to mated individuals.

The stimulus to which the hymenopterous female responds in controlling the sex of her progeny is definitely derived from the environmental conditions existing at the time of egg deposition; that is, the production of females in contrast to the production of males results from the stimulation of the spermathecal gland. The gland, however, secretes only in response to environmental stimuli that are within a certain range of intensity. The intensity of the stimulation is a function of the spatial, meteorological, or chemical nature of the environment at the moment of oviposition.

THE ATTAINMENT OF CASTE

In the progressive evolution of the social Hymenoptera the worker characteristics may have occurred in the following sequence: first, reproductive diapause, then division of labor, and finally morphological differentiation (Flanders, 1953).

It is highly probable, as demonstrated by Bier (1954) in his classic study of *Formica rufa,* that the worker caste develops from eggs that have been undernourished prior to ovulation. Undernourishment is indicated by a reduced amount of yolk in the "ripe" egg and the extension of the preovulation period of such eggs. The physiological conditions supposed to cause this change in status are the precocious deterioration of the nurse cells (Bier, 1954) and the partial absorption of the ripe ovarian egg (Flanders, 1953). These conditions appear to be environmentally induced.

Environmental temperatures may determine the occurrence of undernourished ovarian eggs, as reported for *Formica rufa* (Bier, 1954). This phenomenon may also occur in the wasps. According to Deleurance (1950), the overwintering female of *Polistes* may start her colony more or less simultaneously with two types of female progeny. Although morphologically alike, one type is a worker, the other a reproductive. The occurrence of the worker appeared to be induced by median temperatures, that of the reproductive by the extremes of temperature. The ratio of queens to workers in the stingless bees (*Melipona* spp.) varies with en-

vironmental temperatures (Kerr, 1946), a ratio possibly derived from the relation between the rate at which eggs are generated and that at which they are deposited. Since all individuals as larvae receive equal amounts of food the *Melipona* queen is likely to be smaller than the worker because of the greater nutritional needs of the ovaries.

In the colonies of the ant *Rhizomyrma fuhrmanni* Forel, an obligate coccidophile, it is probable that the occurrence of caste-initiating undernourishment in the ovarian egg is regulated by the humidity of the nest. This is indicated by the following colony conditions as recently observed by the writer in central Colombia: (1) the monophagic subsistence of the ant on a species of the root-feeding coccid near *Eumyrmoccoccus smithi* Silv. and the regulation of the entire coccid population in the area according to the nutritive needs of the ant population, and (2) the constant temperature of the nest throughout the year; estimated to be 21° C. plus or minus one degree (Flanders, 1957a).

In the regressive evolution of the relatively few parasitic species, the "dwarfing" of the individual apparently proceeded to the point at which developmental caste-initiating undernourishment rarely if ever occurs. In such species workers are few or absent.

THE REALIZATION OF SEX AND OF CASTE AS SYNCHRONOUS PHENOMENA

The nature of the environment during the period of oviposition regulates the occurrence of the castes as well as of the sexes so that sex control and caste control are more or less synchronized.

The realization of the worker caste occurs when nest conditions are indigent. The reproductives, queen and male, are fully nourished, a sign that nest conditions have been or are opulent. The occurrence of indigent or of opulent nest conditions appears to be determined by the environmental circumstances that also regulate the activation of the spermathecal gland, full nourishment being associated with the inactivation of the spermathecal gland, undernourishment with its activation.

In the honey bee and the army ant, the conditions that inhibit the activation of the spermathecal gland initiate a sequence of events that results in the full nourishment of the individual.

In the primitive species of ants, bees, and wasps in which the castes lack marked morphological differentiation, it is probable that most, if not all, of the workers remain in a nongravid (neotenic) condition until the colony either lacks a queen or the queen ceases the deposition of fertilized eggs. When such a situation occurs, oogenesis may be initiated in one or more of the adult workers. Presumably, the worker that first mates after attaining a gravid state receives additional food and takes on the status of a queen, thus re-establishing the colony conditions which inhibit and depress ovarian development in the unmated female.

The reversal of the reproductive status of the adult female undoubtedly takes place much less readily when the morphological differentiation of the castes is sufficient to prevent mating. In strongly polymorphic species the reversal in caste may be limited to the larval stage, provided that the predisposition of caste initiated in the ovarian egg is not firmly established and can be nutritionally counteracted (Bier, 1954; Brian, 1954).

Caste, however, may be regulated in the larval stage only in species having a stereotyped colony condition (either structure or behavior) which usually prevents full feeding during that stage. Such a condition is exemplified in the honey bee by brood cells of constant size but so small that the larva developing in each cannot be fully fed. In the tropical army ant, *Eciton* s. str., the absence of full nourishment during the larval stage is usually insured by a constant adult worker-larval brood ratio brought about by the regular occurrence of discrete broods which arise usually with little if any mortality from large batches of eggs deposited periodically, the number of eggs in each batch being practically constant (Schneirla and Brown, 1952).

The queen of the honey bee develops in an extra-large brood cell which permits her to be fully nourished (Haydak, 1943). The queens of the tropical army ant occur when an occasional brood is bisexual and this brood in its egg stage or early larval stages is reduced 90 per cent by cannibalistic action of the attending workers, this action apparently being a more or less indirect response to the environmental factors that inhibited the action of the spermathecal gland. The remaining members of such a brood develop under opulent conditions; males and females are then more or less fully nourished, and the latter become queens.

THE DESTINY OF THE OVULATED EGG IN RELATION TO CASTE

In the Hymenoptera the normal male is derived only from the unfertilized egg. With species in which at all times the secretion of the spermathecal gland can keep pace with oviposition, the fully mated female produces males only when gland stimulation during oviposition is lacking.

In the queen of the social species the inactivation of the spermathecal gland may be an effect not only of the absolute character of the environment, as appears to be the case in *Formica rufa,* but of a change in that environment from the usual to the unusual, from the accustomed to the unaccustomed, as is apparently the case in the honeybee and the army ant. Because of this apparent preferential nature of the fertilization and nonfertilization of the egg, it is possible for the male to continually escape exposure to conditions that initiate polymorphism (Flanders, 1946).

The lack of castes in the male may result from the fertilization of all eggs that are deposited under indigent nest conditions. In many species the ovarian eggs that are undernourished and then ovulated are usually, if not always, fertilized and consequently are workers. Caste differentiation is limited to the female, because the male either develops under opulent nest conditions, is inherently lacking in susceptibility to caste-determining undernourishment, or possesses a threshold of undernourishment so relatively low that caste is rarely realized.

In all of the social Hymenoptera the completely absorbed eggs constitute a large percentage of the total number of eggs generated. Consequently it is significant that with the species having numerous ovarioles the determination of the biparental queen is limited to the larval stage (Flanders, 1957b).

In such species it is logical to assume that all of the deposited eggs have been subjected to caste-initiating undernourishment (regardless of environmental conditions) and that as a consequence the full-nourishment of the larva quantitatively or qualitatively is necessary for the production of biparental queens. Social systems such as those of the honey bee and the army ant are essential for the segregated feeding of the larvae (either in space or in time), and the development of a certain proportion into queens.

The limitation of caste regulation to the larval stage and the development of biparental queens only from eggs predisposed to become workers may be characteristic of species in which colony reproduction takes place only by swarming. In such species the worker, having few ovarioles, may deposit eggs which are yolk-replete and are not reduced in size. Occasionally unfertilized eggs from workers become (uniparental) queens (Flanders, 1945).

It is probable that in all species of the social Hymenoptera the worker develops from an undernourished egg. An egg not thus predisposed to become a worker rarely if ever does so, yolk-replete eggs being deposited when colony conditions are opulent and consequently usually unfertilized.

As suggested by Schneirla and Brown (1952), in the army ant the order of egg deposition in the formation of any brood may establish regular graduated differences in ovisorption susceptibility and thus furnish a basis for the relative differences in attainable size and (in fertilized egg) polymorphic threshold.

It is evident that the trophic mechanisms involved in the realization of caste in the social Hymenoptera are pre-larval, larval, and post larval.

THE ATTAINMENT OF CASTE RATIOS

Continuity of reproduction necessitates the simultaneous occurrence of queens and males. It is obvious that the recurrent periods of indigent and opulent nest conditions determine the ratio of workers to reproductives. The mechanisms involved function also in determining the ratios of queens to males and of queens to workers.

The deposition of eggs destined to develop under opulent conditions and consequently to become males and biparental queens occurs when the secretion of sperm-activating fluids by the spermathecal gland is inhibited. It is the fertilization of the egg under such circumstances which insures the simultaneous occurrence of the reproductive forms and determines the ratios of the sexes and of the castes.

On the basis of studies by Flanders (1939), Hagen (1954), and Schneirla and Brown (1952), it appears that the fully nourished female or queen is usually derived from an egg fertil-

ized by a residual sperm—that is, a sperm which was activated during oviposition under environmental conditions that stimulate the spermathecal gland, but which was in the sperm duct enroute to the oviduct when such oviposition ceased and was not used until oviposition was resumed under conditions that inactivate the spermathecal gland and induce full nourishment of the developing individuals. The egg that the queen honeybee deposits in the preconstructed queen cell, for example, is fertilized by a sperm activated during her oviposition in worker cells (Snodgrass, 1956). The larva from that egg is full-fed.

The queens produced by the tropical army ant are limited to broods originating under certain dry-season conditions that inhibit the activation of the spermathecal gland. The first eggs deposited are the only eggs of this brood that receive sperms (Schneirla and Brown, 1952). This is satisfactorily explainable only on the hypothesis that the sperms thus used were residual sperms held over in the sperm duct after the fertilization of the eggs of the preceding all-worker brood. The spiral convolutions of the spermathecal duct in this species appear to be an adaptation for this purpose (Hagen, 1954).

In the small fallow ant, *Formica rufa,* which produces queens and males when the queen is subject to cool weather (Bier, 1954), the eggs that develop into queens presumably are fertilized by residual sperms. At temperatures of 15.5° C. the spermathecal gland is not activated and the ovarian eggs are not subjected to caste-initiating undernutrition (Gösswald and Bier, 1955). The egg, if then fertilized, would necessarily have received a residual sperm that had moved into the sperm duct when temperatures were higher and workers were being produced.

In species such as *Formica rufa*, it is probable that the numbers of queens relative to the males would vary inversely with the duration of the period of opulence—the shorter the period, the greater the proportion of queens.

RESUMÉ

In species of social Hymenoptera possessing a system for differential larval feeding as in the army ant and the honey bee, each ovulated egg is predisposed to become a worker and does so if it is fertilized and the resultant larva is not fully fed.

In species that lack a system for differential larval feeding only a part of the ovarian complement of eggs is subjected to caste-initiating undernourishment, a differentiation which is presumably an effect of a differential retention of the mature ovarian eggs.

In all species environmental conditions that inhibit the action of the spermathecal gland are conducive to colony opulence and the full nourishment either embryonically or larval of one or more individuals and consequently to the production of queens as well as of males. The fertilized yolk-replete egg may become a queen regardless of subsequent nourishment.

Under opulent conditions the fertilization of an egg is accomplished by a residual sperm—that is, a sperm which was in the sperm duct enroute to the oviduct when oviposition under circumstances that stimulate the spermathecal gland ceased, and hence was not used until oviposition was resumed under circumstances which inactivate the spermathecal gland.

Consequently, in most if not all of the social Hymenoptera the worker is usually derived from an egg which at the moment of ovulation had a reduced amount of yolk. The predisposition of such an individual to be a worker may be nutritionally counteracted during either the larval or adult stages. It then becomes a queen.

CONCLUSION

It is concluded that the castes in the social Hymenoptera usually originate as follows: the worker from a fertilized egg which when ovulated had a reduced amount of yolk; the queen from any diploid egg, provided that the larva from a fertilized egg with a reduced amount of yolk is full-fed; the male from any unfertilized egg regardless of its yolk content. The ratio of females to males is apparently a function of the relative lengths of the periods of indigence (activation of the spermathecal gland), and of opulence (inactivation of the spermathecal gland). In most species the ratio of queens to workers appears to be a function of the number of eggs fertilized by residual sperms during the period of opulence, this number being determined either by the actual number of residual sperms or by the duration of the period of opulence prior to the utilization of all the residual sperms.

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